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Fishing pressure on U. S. reservoirs is increasing rapidly and may double in the next 20 years. To meet increasing fishing demands, effective practical plans must be implemented to maximize and prolong the high sport-fish production that characterizes new impoundments. This report reviews literature on fishery resource development and fish production in new reservoirs and provides guidance on filling and site preparation techniques that should enhance fish production and angling quality.

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During filling, reservoirs are extremely productive because virtually all allochthonous nutrients, detritus, and drowned terrestrial animals, as well as autochthonous production (primary and secondary), are retained in the basin. After a new impoundment is filled, fish production and harvest are high for the first 5 to 10 years but progressively decline as the reservoir ages. Strong year classes of fish may be produced in years of increased precipitation which increases inflow of nutrients and detritus from the drainage basin and raises the lake level to inundate woody vegetation, forest litter, and/or herbaceous plants. Declines in reservoir fisheries primarily result from the losses of nutrients and detritus to outflow and sediments and from the use of detritus by invertebrates and fish.

Concerns during filling include timing of inundation and control of water levels. Because most riverine fishes have evolved reproductive strategies cued to spring floods, filling that resembles natural spring flooding is often the most successful in increasing fish production. Waters that have recently risen to inundate terrestrial vegetation when water temperatures are about 11°C (warmwater fish communities) or 5°C (coolwater fish communities) should greatly enhance spawning success and survival of young-of-year fishes by providing suitable spawning sites, food, and cover. Stage filling (filling to well defined successive pool levels) can be an effective tool to increase fish production, but it is seldom practical except in large storage reservoirs that are built in areas where consumptive needs do not exceed the amount of water that can be supplied at successive stages.

Concerns for reservoir clearing depend on trade-offs among factors such as mosquito control, water quality, recreation, and fish production. Herbaceous plants and forest litter provide an enormous source of food for many microorganisms, zooplankton, benthos, and for some fish. In addition, herbs provide cover for young fish and spawning sites for adults. Woody vegetation provides cover for prey and young sport fish, and the amount of cover influences feeding efficiency and therefore the energy flow through predatory sport fish. Submerged timber, artificial shelters and other structures also concentrate sport fish to improve harvest. On the basis of biological observations, practical methods of clearing reservoirs are presented, but the effectiveness of various methods has not been evaluated, because of insufficient quantitative data. Nevertheless, on the basis of available literature, it is clear that the best clearing plans are those in which all herbaceous plants and forest litter are retained and where timber is retained in selected sites (coves, embayments, along old creek channels, in blocks, or in clusters). However, hazards to navigation and recreational usage should be kept in mind when considering leaving timber in place. A procedure for retaining blocks of timber along steeper shorelines is described. Construction of artificial structures presently cannot be justified monetarily for most new reservoirs in forest regions, where selective retention of timber may provide adequate, maintenance-free structure for no direct cost. In prairie regions, however, artificial structures may be justified and could greatly improve sportfishing.

PREFACE

This report was prepared by the U. S. Department of the Interior, U. S. Fish and Wildlife Service, National Reservoir Research Program (NRRP), Fayetteville, Arkansas, for the U. S. Army Engineer Waterways Experiment Station (WES) under Intra-Army Order No. WESRF-80-210 dated 30 January 1980. This study forms part of the Environmental and Water Quality Operational Studies (EWQOS) Program, Work Unit IIF, Reservoir Site Preparation. The EWQOS Program is sponsored by the Office, Chief of Engineers, and is assigned to the WES under the purview of the Environmental Laboratory (EL).

The review and guidance were written by Mr. G. R. Ploskey for the NRRP. The critical review and recommendations provided by Mr. R. M. Jenkins, Director, NRRP, and Mr. L. E. Vogele and Dr. L. R. Aggus, also of NRRP, are gratefully acknowledged.

The study was under the direct WES supervision of Dr. D. Gunnison, and the general supervision of Dr. R. M. Engler, Chief, Ecological Effects and Regulatory Criteria Group, Dr. R. L. Eley, Chief, Ecosystem Research and Simulation Division, and Dr. J. Harrison, Chief, EL. Dr. J. L. Mahloch was the EWQOS Program Manager.

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CONTENTS

CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI)
UNITS OF MEASUREMENT

U. S. customary units of measurement can be converted to metric (SI) units as follows:

Multiply	By	To Obtain
acres	4046.873	square metres
feet	0.3048	metres
inches	2.54	centimetres
tons (2000 lb, mass)	907.1847	kilograms

FACTORS AFFECTING FISH PRODUCTION AND FISHING QUALITY IN NEW RESERVOIRS, WITH GUIDANCE ON TIMBER CLEARING, BASIN PREPARATION, AND FILLING

PART I: INTRODUCTION

1. Although the number of reservoirs in the United States has increased linearly over the last 20 years, average surface area has progressively decreased. In an inventory of U. S. reservoirs that exceed 500 surface acres,* Ploskey and Jenkins (1980) listed 1608 reservoirs, totalling 9,856,000 acres at average pool elevations. Excluding the Great Lakes, this acreage exceeds that of natural lakes in the contiguous United States (Jenkins 1979). According to projections in the 1980 inventory, about 600 new reservoirs will be constructed by the year 2000, but the area of each will average only 1800 acres.

2. Fishing pressure on reservoirs continues to increase. Total angler-days of pressure in 1974 was about 105 million--a number 2.5 times greater than the total attendance at all collegiate and professional football games in 1973. The National Reservoir Research Program estimates that reservoirs currently receive 200 million angler-days of pressure annually--about one third of the total in fresh waters of this country. Projections for the year 2000 are for 400 million angler-days on an estimated 11 million acres. On this basis, annual fishing pressure on reservoirs will increase from 20.3 to 36.4 angler-days per acre over the next 20 years.

3. According to Study Report No. 7 "Sport Fishing--Today and Tomorrow" (U. S. Bureau of Sport Fisheries and Wildlife 1962), about nine million acres of new reservoirs greater than 500 acres and a doubling of harvest per acre would be required between the years 1960 and 2000 to

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* A table of factors for converting U. S. customary units of measurement to metric (SI) units if presented on page 3.

meet angler demands. Though some gains have been made, the national, area-weighted harvest of sport fishes has not increased greatly in the last 20 years, and over the next 20 years, reservoir area will fall 4.5 million acres short of that required to meet projected demands for fishing at the turn of the century.

4. To meet future angling demands, fishery biologists must employ all available effective techniques to increase the production and harvest of reservoir fishes. Several techniques that have rarely been used to their fullest potential are associated with the construction and filling phases of new reservoirs. Few attempts have been made to selectively retain terrestrial vegetation in reservoir littoral (i.e., the nearshore zone between the surface and a depth of about 5 m), though inundated vegetation provides feeding, spawning, and refuge sites for many fishes. Stage filling of reservoirs, with concern for seasonal timing of inundation and water-level fluctuations during filling, is a promising but relatively new and untested technique.

5. Procedures for site preparation (e.g., clearing and burning timber and soil scraping) are used primarily to improve water quality (Allen 1960; Sylvester and Seabloom 1965; Campbell et al. 1975) and in certain geographical areas, to control mosquitos (Federal Security Agency et al. 1947). Secondary reasons include reservoir navigation (Dussart et al. 1972), aesthetics (Friedrich 1959), and considerations for fish and wildlife (Jenkins 1970b, 1970c; Nelson et al. 1978). Procedures have been developed to reduce impacts of filling on water quality (Sylvester and Seabloom 1965), and minimum pools most often have been set on the basis of anticipated requirements for flood control, power generation, and instream navigation (Wiebe 1960).

6. For fishery management, procedures for site preparation and filling should be designed to maximize and prolong the high fish production that characterizes new impoundments, without sacrificing water quality or severely compromising other major uses. Plans for retention of some timber should be developed to improve long-term harvest of important sport fishes after production stabilizes at lower levels.

7. Cooperation between biologists and engineers is crucial to

the implementation of site preparation and filling procedures that will maximize fishery resources and still meet water quality standards or other use requirements. During the engineering design phase (Dussart et al. 1972), extensive field studies should provide details of one or more accepted options. Early participation by fishery biologists in project planning and provision of more precise information on biological requirements will result in better accommodation of fishery needs (Jenkins 1970c).

8. The purpose of this report is to review factors that affect fishery development and production in new reservoirs and to provide guidance (or sources of guidance) for field offices of the U. S. Army Corps of Engineers. On the basis of available literature, guidance is provided on timber clearing, basin preparation, and filling as related to fishery resources. Where literature was insufficient to provide documented guidance, or was lacking, recommendations were based on the professional judgment of fishery biologists of the National Reservoir Research Program.

9. This report is composed of three parts, the first of which is this introduction. Part II consists of a literature review in three parts: (a) documentation of biological events that characterize the history of most reservoirs; (b) discussion of factors related to filling; and (c) discussion of factors related to "structure" (terrestrial vegetation and artificial shelters). Part III consists of guidance and recommendations derived from the literature review or from discussion with the staff of the National Reservoir Research Program.

10. The literature review and guidance mainly pertain to river reservoirs (flood control, hydropower, or storage) and exclude most data from impounded natural lakes. Grimas (1967) concluded that the development of trophic systems in impounded natural lakes followed a pattern different from that in river reservoirs. Apparently, production is favored in river impoundments but not in regulated natural lakes. Specific plans for different types of reservoirs or for reservoirs in different regions of the United States were not developed because insufficient information is available to support such plans. However, as Wood (1951)

noted, certain principles of management are applicable to all types of large impoundments, and a general management plan suitable for one type may be modified to assist in the management or at least understanding of others. Because the primary goal of this report is to provide guidance on site preparation and filling to improve reservoir fisheries, effort was concentrated on fish and factors affecting them. Brief discussions of nutrient sources, algae, and aquatic invertebrates are presented only to provide a trophic perspective of reservoir ecosystems.

PART II: LITERATURE REVIEW

Fishery Development and Decline

11. A pattern of high biological production followed by a gradual decline and stabilization at intermediate or low levels is outstanding in the history of most reservoirs (Ellis 1937; Baranov 1961; Frey 1967; Dussart et al. 1972; Wright 1973). Baranov (1961) described three phases of productivity in Russian reservoirs. Phase I was termed "trophic upsurge"--a period of high production lasting 2-3 years after inundation. Phase II was described as "trophic depression"--a period of decreased production lasting up to 30 years, and Phase III was defined as a period of gradually increasing productivity, apparent after about 20 years. According to Dussart et al. (1972), the most striking feature upon filling is the sudden beginning and rapid development of the lacustrine system:

> The cycle of biological production is fueled initially, at least, by a microbiological population explosion in the new standing-water habitat. This explosion releases nutrients from the submerged organic matter which is quickly cycled (in days) into primary production--the initial harnessing of solar energy by planktonic algae. With differential rapidity, depending, among other things, on latitude and on the food web involved, this upsurge in primary production is typically transferred through the food chains to a rapid rise in fish production, often with a consequential convergence of fishermen.

However, as the reservoir ages, fish harvest and the number of fishermen generally decline. Duration of the initial "biological boom" apparently varies among reservoirs but usually lasts 2-10 years (10-15 years--Allen 1960; 2-3 years--Baranov 1961; 5-10 years, with a few up to 25 years--Cooper 1967).

12. Frey (1967) described the pattern of decreased production as follows:

> After these spectacular surges of all biological processes during the first couple of years, probably

> controlled mainly by the utilization of terrestrial organic matter, conditions begin to stabilize at lower levels. Phytoplankton generally declines, benthos becomes less abundant and with a different species composition, and fish populations drop off.

Bacteria and algae

13. Increased production occurs at all trophic levels simultaneously but is most rapid among microorganisms due to their high rates of turnover. Many authors have written of population explosions of algae and bacteria (e.g., Irwin 1945; Baranov 1961; Frey 1967; Campbell et al. 1975). Benson and Cowell (1967) observed high densities of green flagellates when water first inundated terrestrial areas of new Missouri River reservoirs. Rodhe (1964) reported that primary production increased slightly during filling of a Swedish reservoir but that large increases of 2-3 times required two years. During the inundation of a Canadian reservoir, Duthie and Ostrofsky (1975) observed an initial decrease in areal primary production and algal biomass, as a result of high turbidity and dilution, respectively. After turbidity decreased and light was no longer limiting, algal production increased severalfold.

Aquatic invertebrates

14. Sources of reservoir benthos (Ioffe 1961) and zooplankton include the river, standing water within the basin, and nearby bodies of water. Colonization by benthic insects (e.g., Diptera, Ephemeroptera, Odonata, and Trichoptera) may be accomplished by winged terrestrial adults that actively disperse and deposit eggs in new impoundments. Molluscs can disperse actively throughout an entire drainage, but most probably disperse passively as eggs or larvae carried by floodwaters, birds, or fish (e.g., parasitic glochidial larvae of pelecypods). Other benthic invertebrates such as oligochaetes and nematodes migrate throughout entire drainage systems or disperse passively as resistant eggs, cocoons, or cysts. Zooplankters also may passively disperse overland as eggs or cysts that are resistant to desiccation. Wind and terrestrial animals associated with water commonly act as vectors for passive dispersal. Colonization by invertebrates may be rapid (less than 6 months--Davis and Hughes 1966; 2-4 months--Paterson and Fernando 1970; 1-3

months--Aggus 1971) and frequently is dominated by littoral zooplankton and benthos (Aggus 1971; Starzykowa 1972; Armitage 1977; McLachlan 1977).

15. Zooplankton numbers and biomass usually increase greatly during inundation of new reservoirs (Wright 1954; Krzanowski 1971; Duthie and Ostrofsky 1975). Axelson (1961) observed a marked increase in the density of zooplankton after regulation of a natural lake. Although numbers seemingly increased during filling of Lake Oahe, North and South Dakota (June 1976), abundance decreased after filling because water discharge increased. Starzykowa (1972) found that the magnitude of zooplankton production was greater in new reservoirs than in old and also greater in impoundments with low rather than high rates of water exchange. Mean annual standing crop of zooplankton during filling of Beaver Reservoir, Arkansas, (33.4 $mg \cdot m^{-3}$) was not significantly higher than that in Bull Shoals Reservoir, Arkansas, (28.2 $mg \cdot m^{-3}$) after 14 years of impoundment (Applegate and Mullan 1967c, 1967d). However, zooplankton in Beaver Reservoir exhibited a bimodal seasonal distribution of biomass; whereas, the seasonal pattern of biomass in Bull Shoals was unimodal. The authors suggested that the bimodal distribution of biomass in Beaver Lake may have contributed more to fish production than the unimodal distribution in the older impoundment.

16. Midges (Chironomidae) usually dominate the benthos of new reservoirs. Ioffe (1961) noted that midges often compose 50 percent or more of all benthic species. Davis and Hughes (1966) found that many midges followed rising waters during filling of Bayou D'Arbonne Reservoir, Louisiana, and dominated the benthos within six months. Midge populations in excess of 34,000 m^{-2} developed in the first year of impoundment of Kuibyshev Reservoir, U.S.S.R. (Frey 1967). During filling of Laurel Creek Reservoir, Canada, Paterson and Fernando (1970) observed an increase in total midge density from ca. 200 m^{-2} in April to ca. 10,000 m^{-2} in June. Similar observations of the domination of new reservoirs by midges were made by Aggus (1971) and McLachlan (1977).

Fish

17. High productivity of reservoirs during and for 5-10 years

after inundation also is reflected in the abundance and harvest of fish. Examples include large numbers of sport fishes during the early years of Claytor Lake, Virginia (Roseberry 1950); Upper Spavinaw Lake, Oklahoma (Jackson 1958); Lake Francis Case, South Dakota (Gasaway 1970); Lake Oahe, North and South Dakota (June 1976); Red Rock and Rathbun Lakes, Iowa (Paragamian 1977), and West Point Lake, Alabama and Georgia (King et al. 1979). Fishing success was fair to excellent during early years of impoundment of Lake Stockton, Missouri (Goddard and Redmond 1978). Catch rates in Lake Francis Case, South Dakota (Gasaway 1970) were highest--1.37 fish per hour--shortly after filling (1954) but declined to 0.27 fish per hour in six years. Catches of sport fish from Beaver Lake, Arkansas, declined from 0.59 kg per angler-hour shortly after impoundment (1965) to 0.14 in 1979 (National Reservoir Research Program 1980). June (1976) considered the initial commercial and sport fisheries to be good in Lake Oahe from impoundment in 1958 to 1968, but noted declines from 1969 to 1974. Creel surveys on Rough River Reservoir, Kentucky, before and after impoundment, showed that sportfishing success was greater in the new reservoir than in the river, but that harvest decreased each year after impoundment. Jenkins (1968), who analyzed harvest data from 121 U. S. reservoirs, found that sport fish harvest was inversely related to reservoir age.

18. Dussart et al. (1972) described age-related changes of harvest in two large African reservoirs. In Lake Kariba, the fishery developed rapidly after inundation, and within five years roughly 2000 local fishermen were landing 4000 short tons of fish annually. After 10 years of impoundment, harvest from Lake Kariba had dwindled to 1000 short tons per annum, and the number of fishermen had decreased markedly. Observations were similar at Volta Reservoir.

19. The production and harvest of fish depends on many factors including reproductive success, growth, and recruitment. The 1975-76 harvest of largemouth bass from the 1975 year class in West Point Lake, Georgia and Alabama, (King et al. 1979) was exceptionally high (22.4 kg/ha). This harvest reflected successful spawning, high survival, and rapid growth--up to 300 mm in the first year of life (Shelton et al. 1979).

Rapid growth is a distinct advantage to young-of-year (YOY) fish because they quickly become too large to be eaten by yearling predators. Enhanced survival increases the numbers of fish recruits, and rapid growth shortens the time required to provide fish of a harvestable size.

20. Rapid growth is characteristic of most fishes after filling. Channel catfish grew rapidly during the first three years in Tenkiller and Fort Gibson Reservoirs, Oklahoma (Jenkins and Leonard 1954). Game fish of Norris Lake, Tennessee, also grew rapidly through the fifth year of impoundment (Eschmeyer and Jones 1941), but rates were highest during the first three years (Stroud 1948). Jackson (1958) noted that largemouth bass, white crappie, gizzard shad, and spotted sucker grew faster in a new than in an old Oklahoma impoundment. The growth of most species of sport and commercial fishes was fastest in the first few years after filling of two Iowa reservoirs (Paragamian 1977). Jenkins (1979) noted that surplus production is high in new reservoirs, and that most of it is contributed by a few short-lived species of prey.

21. Duration and intensity of productive periods vary among reservoirs, and this fact suggests that controlling factors related to filling and site preparation exist. Knowledge of what the controlling factors are, how they function, and whether they can be manipulated is essential to the development of effective guidance on site preparation and filling.

Factors Related to Filling

22. An enormous volume of literature exists on water-level manipulation and its effects on reservoir biota. An annotated bibliography of papers related to minimum pools and fluctuation of water levels was published by the Food and Agriculture Organization (FAO) of the United Nations (Fraser 1972). Another unpublished annotated bibliography was completed in 1980 by the Ohio Cooperative Fishery Research Unit, Columbus, Ohio. Though a review of water-level manipulation as a management tool to enhance fisheries is beyond the scope of this report, results obtained by such practices are instructive because they are similar to those

obtained when reservoirs are first filled.

23. Keith (1975) summarized observations of many fishery biologists who have studied effects of water-level fluctuations when he listed four major results produced by increases in water level, i.e., the flooding of terrestrial vegetation around the shoreline of a lake:

- a. It initiates the death and decomposition of vegetation and release of nutrients which increase the water's productivity.
- b. It immediately adds numerous fish food organisms to the water, such as insects, earthworms, and other small terrestrial animals.
- c. It temporarily creates excellent cover and desirable habitat for shoreline dwelling fishes.
- d. It creates an area of water that is initially sparsely populated with fish life, a condition which stimulates the natural reproductive and growth process of the resident fishes.

Keith equated these conditions to those existing in new reservoirs. King et al. (1979) listed three factors that contributed to the "boom and bust" sequence of fishery development in West Point Reservoir: (a) flooding of rich bottom lands increased fertility; (b) inundated vegetation and other structure provided cover; and (c) rising waters increased space for expanding fish populations.

Nutrients and organic detritus

24. Nutrient availability is part of a popular hypothesis that accounts for the sequence of biological events in reservoirs. Many biologists have emphasized the importance of nutrients released from inundated soils and terrestrial vegetation (Ellis 1937; Wood 1951; Allen 1960; Neel 1963; LeCren 1965; Cooper 1967; Dussart et al. 1972; Campbell et al. 1975; Keith 1975; Nelson et al. 1978). Ellis (1937), for example, envisioned a new reservoir as analogous to a large "hay infusion," wherein favorable biological conditions are produced by the solution of nutrients (N, P, and ionizable salts) from organic debris left on the floor of the basin. Wood (1951), who reviewed much of the early literature on water-level management, stressed the importance of nutrients, primary producers, and trophic transfer. Baranov (1961) discussed

findings from Soviet reservoirs, which indicated that food resources in new reservoirs were proportional to the amount of vegetation flooded. He also emphasized nutrient relations and trophic webs. Dussart et al. (1972) attributed increased fish production and harvest to abundant nutrients (leached from organic materials), increased primary production, and trophic transfer. Other biologists who have reported similar observations include Stroud (1948), Roseberry (1950), Wright (1954), Ioffe (1961), Nelson et al. (1978), and King et al. (1979).

25. In this "nutrient-trophic hypothesis," the decline in fish production after several years results from a loss of nutrients to sediments, outflow, and fish harvest. However, the simplicity of this hypothesis may be misleading, because many other factors affect fish production, such as nutrient inflow, water depth, mixing, drawoff, turbidity, rates of volume displacement, fluctuation of water level, and the expanse of water over benthic soils (Cooper 1967).

26. The value of the "nutrient-trophic hypothesis" may have been overemphasized by many biologists, inasmuch as the energy flow through detrital pathways may equal or exceed that moving through living food webs. Although primary production generally increases after a reservoir is filled, it often requires several years to peak. Primary production may even decrease initially (Duthie and Ostrofsky 1975; Hecky 1980) due to high turbidity and then gradually increase severalfold in a few years after impoundment. Though a decline in fish production in reservoirs is almost universal and the initially high production has been attributed to organic matter and nutrients from the basin, studies in Bighorn Reservoir, Montana and Wyoming, showed that phytoplankton production increased steadily after impoundment (Wright 1973). McCammon and von Geldern (1979) stated that reservoir fertility does not diminish with age; however, fertility does vary with inflow, which is largely a function of precipitation. The idea of increasing algal productivity as reservoirs age is more consistent with the concept of eutrophication than is that of decreasing productivity.

27. Consumption of organic detritus by some invertebrates and fish probably is as important as the leaching of nutrients from

vegetation and soils. The initial surge of secondary productivity by invertebrates and forage fish may be largely a function of energy transfer through detrital pathways. Declines in fish production after 5-10 years may not result as much from a seldom-observed decrease in total algal productivity, as from the use of available organic detritus by biota and loss of detritus to sediments and outflow. Most benthic animals that initially colonize impoundments are detritivores and omnivores, e.g., chironomids and oligochaetes (Ioffe 1961). McLachlan (1977), who studied food habits of benthos in three reservoirs, noted that inundated organic matter was a major food of over 500 insect larvae (primarily chironomids) before, during, and after filling. Data from two of the impoundments indicated a sharp decline of allochthonous foods in insect diets (from 93 to 64 percent, and from 89 to 52 percent) after the reservoirs were filled. Decreased consumption of detritus corresponded well with an overall reduction of benthos after filling. McLachlan concluded that reduced benthos densities were due to a dietary change from detritus to algae. Aggus (1971) observed that densities of benthos were greatest in areas of flooded herbaceous plants (e.g., old field grasses)--apparently their primary source of food (directly or indirectly). Diets of nonpredatory zooplankton frequently include large quantities of detritus (Smirnov 1962, Andronikova et al. 1972), and Gutel'mackher (1973) determined that dispersed bacteria composed 28-38 percent of the diets of <u>Bosmina longirostris</u>, <u>Holopedium gibberrum</u>, and <u>Diaptomus graciloides</u>. Even the gizzard shad, the principal forage fish in many temperate reservoirs, consumes large volumes of detritus (3-66 percent, Kutkuhn 1958; 7.2-82.0 percent, Price 1963; 85.5-86.2 percent, Dalquest and Peters 1966).

28. According to Odum and Herald (1975), the connection between terrestrial primary production and aquatic secondary production often has been overlooked. In many streams and lakes, particles of detritus from tree leaves and twigs are the most important source of plant energy--not phytoplankton or benthic algae. In new reservoirs in forest regions, where large areas of forest floor are inundated, organic litter probably dominates the trophic system during filling and for a few years thereafter.

Dry weight of forest litter (mean = 10,800 kg/ha), as cited by Ovington (1962), exceeds primary production by phytoplankton (mean = 5,250 kg/ha; Likens 1975) in even the most eutrophic lakes. Though detritus may be more important than primary production during early years of impoundment, the large quantities of detritus available throughout the basin after inundation are not renewable.

29. As reservoirs age and the principal source of detritus is inflow from the drainage basin, fish production may fluctuate annually, being higher in years of greater precipitation, when inflowing nutrients and detritus increase. Standing crops of fish that consume large volumes of detritus in DeGray and Bull Shoals Reservoirs, Arkansas, were significantly increased during years of high inflow. Although the biomass of fish that consume small volumes of detritus also increased in most high-water years, they responded to a much lesser extent than did detritivore species, which account for most of the early variation in total standing crop (National Reservoir Research Program, unpublished data).

30. As new reservoirs fill, nutrients (N, P, and trace elements) and detritus enter trophic webs from four major sources: (a) leaching and physical separation from the mixed soils and organic debris--e.g., submerged humus and fallen leaves; (b) leachate and particulate matter from submerged terrestrial vegetation (herbaceous and woody); (c) inflow from the drainage basin; and (d) drowned terrestrial animals. The importance of each source is difficult to demonstrate in situ, as measures of all commonly assayed chemicals (e.g., PO_4, NO_3, Cl^-, SO_4, O_2) often fail to demonstrate a higher nutrient base in new reservoirs (Mullan and Applegate 1966; Applegate and Mullan 1967c, 1967d). Nevertheless, biologists know intuitively that fertility increases because of increased plankton abundance and growth (Neel 1963). Increased nutrient levels may be impossible to demonstrate chemically, inasmuch as nutrients probably are used as soon as they become available.

31. Soils and organic debris. Soils with high organic content cause the greatest degradation of water quality (Sylvester and Seabloom 1965; Sylvester 1965). Whether soils significantly affect fertility

depends on organic content, state of decay, and the geographical extent of fertile soils in the basin.

32. Inundated soils covered with leaves (deciduous forest) or needles (coniferous forest) provide a source of food for benthic detritivores and microfauna. Forest type and seasonal timing of inundation may affect the magnitude and value of this detrital supply. Ovington (1962) observed little accumulation of organic matter on the floor of deciduous forest, while considerable weights of litter persisted in coniferous forests. Yount (1975) found nearly constant ovendry weights of needle litter throughout the year (ca. 1.4×10^4 kg/ha), while weights of litter in a deciduous forest fluctuated significantly, with maxima in November and May (ca. 9.1×10^3 to 1.0×10^4 kg/ha) and minima in September and March (ca. 7.6×10^3 kg/ha).

33. Forest litter is an important source of P and N for reservoir algae, and season of filling may influence the quantity of P and N leached from flooded litter, inasmuch as the contents of P and N in litter vary seasonally. Yount (1975) demonstrated that P and N contents were lowest during September and June (P = ca. 10 kg/ha; N = ca. 85 kg/ha) in hardwood litter and in July (P = ca. 14.7 kg/ha; N = ca. 150 kg/ha) in coniferous litter. Chandler (1941) found that 18.5 and 3.4 kg/ha of N and P, respectively, were returned to soils of a deciduous forest annually. Estimates for a coniferous forest (Chandler 1943) were 26.4 and 2.0 kg/ha•year for N and P, respectively.

34. Vegetation (herbaceous and woody). Inundated herbaceous vegetation also serves as an important source of nutrients and substrate for algae and aquatic detritivores (bacteria; protozoa; some multicellular zooplankton, benthos, and fish). Diets of black bullheads, for example, consisted of a large volume of annual plants (ca. 26 percent) during filling of Beaver Lake, Arkansas (Applegate and Mullan 1967a). Because herbs die rapidly after inundation, they are assimilated into the trophic system as high-energy detritus. Utilization follows the same pattern peviously described for forest litter.

35. Quantities of herbaceous vegetation can be large, especially in grassland regions and in thinned or cleared forest. Pase and Hurd

(1957) showed that air-dried biomass of herbage increased from 25 to 1857 kg/ha when the basal area of trees decreased from 50 to 0 m^2/ha. Though the largest quantities of herbage seldom are as great as the quantity of litter in mature forests, herbage may be more important per unit of weight than litter, because litter generally contains a greater proportion of indigestible matter (i.e., twigs and wood debris with large amounts of cellulose; Sylvester and Seabloom 1965; Ball et al. 1975).

36. Rates of nutrient leaching from inundated vegetation are directly proportional to the ratio of its surface area to its volume. In comparing the 3-day biological oxygen demand (BOD) of different types of vegetation, Sylvester and Seabloom (1965) noted that the high BOD of ferns, leaves, pasture grass, and twigs versus that of wood pieces, demonstrated the effect of exposed surface area. The BOD also depended on organic content and state of decay. Vegetation high in cellulose (e.g., timber) was not readily degraded. The BOD of pasture loam with dead grass was high (10 $mg\ell^{-1}g^{-1}$); whereas, that of gravel loam with wood fragments was much lower (0.24 $mg\ell^{-1}g^{-1}$). Ferns and maple leaves had a greater BOD (7.9 $mg\ell^{-1}g^{-1}$) than did fragments of cedar wood and bark (2.4 $mg\ell^{-1}g^{-1}$), and fresh wood fragments exerted more demand than rotting wood (2.4-2.6 versus 0.9 $mg\ell^{-1}g^{-1}$).

37. Ball et al. (1975) found that vegetation type influenced the rate and quantity of nutrients released. Grasses and herbage released nutrients faster than trees, contained a greater quantity of nutrients per unit of vegetation weight, and were more available in greater quantities (weight per unit area) in the basin of Palmetto Bend Reservoir, Texas. These findings are corroborated by the persistence of dead timber in uncleared portions of some reservoirs--17 years in Beaver Lake, Arkansas, and 30 years in Bull Shoals Lake, Arkansas (personal observation)--and by the almost complete decomposition of herbaceous vegetation in one year (Ball et al. 1975).

38. A review of earlier information detailing effects of inundated terrestrial vegetation on water quality was completed by Ball et al. (1975), who listed the following conclusions:

a. Effects of inundated terrestrial vegetation on water quality are not necessarily permanent but depend on flushing rates, land use, temperature, and basin morphometry.

b. Decomposition rates of vegetation are largely a function of tissue type, and leaves decompose and release nutrients more rapidly than do bark and wood.

c. Phosphorus is rapidly leached from dead, hardwood leaves and particularly from leaves that are damaged or broken.

d. Grasses may be completely decomposed within one year after inundation.

39. Inflow. Quantities of allochthonous nutrients and detritus flowing into a reservoir from the reservoir's watershed are important in determining the biomass of fish that can be maintained. These quantities depend on the concentration of fish in the inflowing river, on rates of inflow, and on residence time of reservoir water (Aggus 1979). Schindler (1971) demonstrated that the nutrient supply of Canadian lakes was a function of drainage area divided by volume. On the basis of an extensive multiple-regression analysis of data from 127 reservoirs, Jenkins (1968) correlated standing crop to total dissolved solids (TDS), shoreline development ratio, and storage ratio. Jenkins (1974) found that among impoundments with similar TDS, those with higher exchange rates supported larger standing crops of fish.

40. The quantity of allochthonous detritus and nutrients washed into a reservoir varies greatly among years as a function of precipitation, but the average influx probably varies little with reservoir age. Low rates of water exchange during filling contribute to the high productivity of new impoundments. During filling of reservoirs, virtually all allochthonous nutrients and detritus, as well as autochthonous primary and secondary production, are retained in the basin. By contrast, operational reservoirs discharge considerable quantities of nutrients, detritus, zooplankton, and larval fish. Benson and Cowell (1967) estimated a wet-weight discharge of 9,058 metric tons (t) of phytoplankton and 12,619 t of zooplankton (less rotifers) from Lewis and Clark Lake, South Dakota, in 1963-64. In 1964-65, the discharge of zooplankton was about 30,000 t, though the volume discharged was similar to that in the previous year. On the basis of minimum and maximum concentrations of

P and NO_3 in this reservoir, from 178 to 56,000 t of P and from 3,027 to 33,838 t of nitrate were discharged in 1963-64. These figures do not include the P or N in discharged organisms.

41. Drowned animals. Terrestrial animals drowned by rising water represent a significant source of fish food during filling of reservoirs. Even as reservoirs age, terrestrial insects from inundated timber and trees adjacent to the reservoir frequently constitute significant portions of the diets of sunfish and other fish (Appendix E of Leidy and Jenkins 1977). Mullan and Applegate (1970), who examined the stomach contents of largemouth bass, spotted bass, bluegill, green sunfish, and longear sunfish during two of the three years of filling of Beaver Lake, Arkansas, found that the volumes of terrestrial organisms in fish were greatest after rising waters first inundated terrestrial soils. Terrestrial earthworms, insects, slugs, spiders, centipedes, sowbugs, and worm snakes were major foods in these seasons. In the two-year study, roughly one-third of the total food volume was terrestrial, composed mostly of earthworms (78 percent) and insects (16 percent). Black bullhead in Beaver Lake switched from a diet of organic detritus, filamentous algae, and crayfish (97 percent by volume) to one dominated by terrestrial animals (56 percent by volume) and detritus (Applegate and Mullan 1967a). After a 1-m rise in the level of a natural lake, trout ate 41 percent terrestrial animals, in contrast to their normal diet of 86 percent aquatic invertebrates (Frost 1956).

42. During filling of reservoirs, drowned animals may be most important to the rapid growth, high survival, and recruitment of fishes than all other nutrient sources. There are no intermediate consumers between fish and this food, consumers that would reduce the amount of usable energy by 80-90 percent. Though the effect may be short-lived, this form of food is efficiently assimilated into fish biomass.

Expanding fish populations

43. Primary and secondary production, detritus, and drowned organisms are important to increased sport-fish production in new reservoirs, but an increased food base is only part of the explanation. Environmental conditions apparently are more important than fecundity in

determining reproductive success. As a reservoir fills, aquatic habitat expands, food and cover are abundant, and competition and predation are low. At this stage the reproductive success of riverine fishes is most important in populating this competitive void. As animals with "boom or bust" reproductive capabilities, which rely on sheer numbers of eggs to produce a few survivors and maintain their species, fish are uniquely adapted to exploit favorable environmental conditions. Because of the inherently high fecundity, a sudden increase in the survival of eggs, larvae, and juveniles can result in the populating of a large reservoir by the progeny from a few adults, during the first year of impoundment.

44. Reproductive success. Riverine fishes apparently have evolved reproductive strategies that are cued to spring flooding. Species that spawn during spring in rivers generally reproduce successfully during early years of impoundment (Benson 1973). Carp, river carpsuckers, bigmouth buffalo, and smallmouth buffalo in Lewis and Clark Lake (Walburg and Nelson 1966) are examples. In Soviet reservoirs, optimum spawning conditions were observed when water levels rose in the spring and remained high or continued to rise (Il'ina and Gordeyev 1972).

45. Spawning success has been attributed to many factors, most of which are related to changes in water level. Species successful in spawning in Clearwater Lake, Missouri, (e.g., brook silverside, bluntnose minnow, bluegill, and longear sunfish) increased greatly after the lake filled (Martin and Campbell 1953). Their success was related to stabilized water levels during spawning, increased suitable spawning area, low predator density, abundant food, and abundant cover. Aggus (1979) noted that timing and duration of flooding influenced the relation between high water and spawning success of many species. Walleye abundance increased as a result of the inundation of clean shoal areas by high water (Chevalier 1977). Johnson et al. (1966) stated that the extent to which clean gravel shoals were flooded in spring determined whether walleyes were forced to spawn on other bottom types where egg survival was poor.

46. Rapidly receding waters may result in desertion of nests, failure of nests, disrupted spawning, or atresia (intraovarian mortality

of eggs) in species that build nests along shorelines (black bass, sunfish, crappie) or spawn in shallow water (perch, northern pike, carp, buffalo, and gizzard shad). Walburg (1976) noted that low water (when spring and early summer water levels declined) adversely affected spawning success of gizzard shad, emerald shiner, white bass, white crappie, and yellow perch in Lewis and Clark Lake, South Dakota. Pelagic spawners such as freshwater drum were unaffected. June (1970) concluded that a sudden lowering of water levels prevented female northern pike from entering previously used spawning areas and increased the incidence of atresia. Rapid significant declines in water levels may cause nest desertion (Buck and Cross 1951; Webster 1954), which increases predation of eggs (e.g., by sunfish; Vogele 1975) or leaves nests and eggs exposed to air (Webster 1954; Heman 1965; Walburg 1976). Poor spawning success of largemouth bass, carpsucker, and channel catfish in Lake Carl Blackwell, Oklahoma, was attributed to declining water levels (Johnson 1973).

47. Siltation in nests is a condition caused by wind-related turbulence in shallow water. Silt on eggs has been observed to increase mortality, and extremely high sediment loads in rising waters during the filling of a reservoir can influence reproductive success. Hassler (1970) found 97 percent mortality of northern pike eggs in clay bluff areas when they were covered by silt at a rate of 1 mm/day. Benson and Cowell (1967) attributed increased survival of young black crappie, white crappie, yellow perch, northern pike, and cyprinids to reduced silting in areas of Lewis and Clark Lake that were protected from the wind. Flooding of terrestrial vegetation decreases erosion and redeposition of sediment by reducing turbulence or by binding soils.

48. Year-class strength of fishes is strongly influenced by survival of larvae and juveniles, and both climatic and biological factors determine their survival. For example, the year-class strength of yellow perch in four Missouri River reservoirs was affected by above-average precipitation which increased the quantity and quality of spawning substrate and reduced predation on young perch (Nelson and Walburg 1977).

49. Strong year classes of many freshwater fish have been correlated with rising water (Buck and Cross 1951; LeCren 1965). Specific

examples include largemouth bass (von Geldern 1971; Summerfelt and Shirley 1978); northern pike (Hassler 1970); saugers (Walburg 1972); and carp, river carpsucker, smallmouth buffalo, and bigmouth buffalo (Gasaway 1970, Elrod and Hassler 1971). By contrast, decreasing or fluctuating water levels can result in poor year-class development. For example, year classes of largemouth bass failed when water levels of Lake Nacimiento, California, were lowered excessively (von Geldern 1971).

50. Water levels determine available refuge by inundating or receding from terrestrial vegetation. Decreasing water levels reduced cover and refuge for larval and juvenile stages of spotted bass (Vogele 1975). Reduced cover usually exposes YOY to increased predation (e.g., black bass--Hogue 1972; Aggus and Elliott 1975). Effects of refuge on predator-prey relations are discussed under the heading "Factors Related to Structure."

51. Standing crop. Jenkins (1970a), who analyzed the effects of selected environmental variables on standing crop of fishes in 140 large reservoirs, found significant correlations of standing crop to several variables (mean depth, storage ratio, shoreline development ratio, TDS, surface area, water-level fluctuation, reservoir age, growing season, outlet depth, and thermocline depth). Of these, growing season is the only variable not directly influenced by construction of dams or filling of new impoundments. Total standing crop (at $\alpha = 0.20$) was positively affected by outlet depth, shoreline development, and TDS. Crops of total sport fish, buffalo, and white crappie were inversely related to mean depth. Lower rates of water exchange (high storage ratios) increased crops of bullheads, channel catfish, largemouth bass, smallmouth bass, and white crappie and decreased those of flathead catfish, bluegill, and longear sunfish. Surface area was positively related to northern pike crop but inversely related to crops of bullhead, sunfish, and black bass. Large annual water-level fluctuations increased crops of flathead catfish, black bass, and white crappie and decreased those of northern pike and sunfish.

52. Some generalizations made by Jenkins (1970a) are as follows:

a. Largemouth bass production hypothetically would be

greatest in a shallow reservoir with a bottom outlet, low rate of water exchange, high TDS, and a long growing season. By contrast, northern pike production would be greatest in a large reservoir with little water-level fluctuation, low TDS, and a short growing season. On this basis, large crops of both species clearly cannot be produced in the same reservoir.

b. Production of white crappie--but not black crappie--parallels that of largemouth bass.

c. Greater total crops are produced in reservoirs with a stable summer thermocline than in those with a weak thermocline, or no thermocline. Largemouth bass and catfish crops were inversely related to the depth of the thermocline, but thermocline depth apparently did not influence the standing crops of other fishes.

Factors Related to Structure

53. Many beneficial effects of reservoir filling can be related to the inundation of terrestrial vegetation. Some species of fish respond favorably to structure, as terrestrial animals do. Many important sport fish build nests for spawning and select desirable substrate, often in or near submerged structures such as brush, logs, stumps, rocks, (Vogele 1975; Vogele and Rainwater 1975). Many larval and juvenile fish (and some adults--e.g., minnows) concentrate in structured areas for refuge from predators. Larger predators concentrate in such areas to feed on concentrations of prey, and possibly because they too prefer diversity of habitat. Bass monitored by radiotelemetry spent 80 percent of their time near artificial reefs (Prince and Maughan 1979). Whatever the reason, concentration of sport fish improves harvest.

54. Beneficial effects of structures are not limited to fish. Standing timber provides habitat for birds (e.g., woodpeckers and waterfowl) and affords fishermen moorage and protection from the wind, as well as privacy and protection from water-skiers and speedboaters (Jenkins 1970c).

Fish food organisms

55. Submerged structures in the littoral zone of reservoirs often are colonized by periphyton and invertebrates, thereby increasing forage available to fish. Littoral zooplankters and bottom organisms, many of

which feed on algae and detritus, are highly productive and provide a good source of food for fish. Claflin (1968) found maximum densities of periphyton on inundated trees in Lewis and Clark Lake at depths of 3 to 7 m. Distribution of macrofauna, composed primarily of midge larvae, was significantly correlated with periphyton density. Maximum densities (April-May) were 10,500 larvae and 4,800 pupae per m^2. Few insects were present on trees at depths exceeding 7 m. Cowell and Hudson (1967) observed that summer densities of chironomids on submerged timber in Lewis and Clark Lake were 11 times greater than mean densities on adjacent bottom areas. In Lake Francis Case, benthos densities were four times greater on timber than on bottom substrates, and in both reservoirs, benthos densities were significantly correlated to the concentration of periphyton pigment.

56. Ioffe (1961) termed the higher production of benthos in submerged forest and shrubs as "characteristic" of nearly all reservoirs, regardless of geographical location. He measured biomasses (wet weight) of 315 g/m^2 on shrubbery (Tsimlyanshoe Reservoir, U.S.S.R.) and 123 g/m^2 on tree surfaces (Rybinsk Reservoir, U.S.S.R.). He found that the biomass was sharply depleted in spring and summer, due to feeding by benthophagous fish. Aggus (1971), who studied benthos development in Beaver Lake, found greater accumulations of benthos in herbaceous vegetation than in areas of flooded timber, but weights in timbered areas exceeded those in cleared areas. Most of the benthic biomass was in shallow water less than 3 m deep. By contrast, littoral areas of 14-year-old Bull Shoals Lake lacked standing timber and herbage; consequently, midges were virtually lacking (Applegate and Mullan 1967b). The authors suggested that the lack of larger midges--forms which may have "bridged the gap" between smaller invertebrates and fish in the diets of largemouth bass in Beaver Lake--resulted in slower growth of largemouth bass in Bull Shoals Lake. In Lake Mead, when large areas of terrestrial vegetation were inundated, zooplankters (primarily Cladocera) became more abundant in littoral areas and in the diets of largemouth bass fingerlings (Allan and Romero 1975).

Fish

57. Reproductive success. Structure is important to the spawning

of nest-building fish, though its exact function is not always clear. Hassler (1970) suggested that high water levels have little positive effect on spawning of northern pike unless suitable vegetation is inundated. Failure of the 1964 year class in Lake Oahe, South Dakota, was attributed to a lack of grass substrate for egg deposition. Beckman and Elrod (1971) correlated yellow perch abundance in Lake Oahe to the availability of brush (on which perch deposit their eggs). Largemouth bass in Lake Mead built nests on a variety of substrates, including bedrock, rootlets of salt cedar, sessile algal mats, rocks, gravel, and rubble (Allan and Romero 1975). No nests were observed on sand or silt. Nests usually were situated close to salt cedar, large rocks, or ledges. In years of high water, spotted bass in Bull Shoals Lake preferred to nest in areas of dense vegetation such as greenbrier, broom sedge, or secondary timber. Nests were usually in small, clear areas, but cover was invariably nearby (Vogele 1975). Vogele (1980) listed a number of structures near which smallmouth bass frequently nested, in order of their importance: large rocks, sunken logs, small waterlogged tree branches, bases of submerged trees, and stumps. About 80 percent of the nests were near cover. In Lake George, Minnesota, 92 of 97 largemouth bass nests located were among bullrushes, on mats of short needlerush, at depths of 0.3-1.2 m (Kramer and Smith 1962). In a western slough of the lake, nests were on needlerush mats, firm humps of fibrous debris, or in pits of soft detritus. On the basis of underwater observations, Vogele and Rainwater (1975) found that spotted bass consistently preferred sheltered habitat for nest building; largemouth bass were more selective of shelter early in the season, during their most intensive nesting period; and smallmouth bass showed no preference for brush shelters but preferred rock and gravel substrate. Vegetation may be a crucial factor limiting nesting success of black crappie, as most spawning occurs at the base of vegetation (Ginnelly 1971).

58. Nearby structure no doubt makes nests easier to defend against egg predators (e.g., sunfish--Vogele 1975, 1980; Vogele and Rainwater 1975), but equally important, it reduces turbulence and erosion of silt that will increase egg mortality or nest failure upon redeposition

(Hassler 1970). Benson (1976) stressed the importance of herbaceous plants in providing spawning sites, refuge, and erosion control. Nest failures of largemouth bass in Lake Mead apparently resulted from erosion of steep shorelines composed of loose materials (Allan and Romero 1975). Survival of largemouth bass eggs in Lake George, Minnesota, was better on substrate with vegetation than on substrate without it (Kramer and Smith 1962). Egg survival was as follows: 25 percent on sand, 58 percent on fibrous humps, 44 percent on needlerush. In a slough, egg survival was even higher (70 percent on sand and 88-94 percent on needlerush), probably as a result of reduced turbulence. McCammon and von Geldern (1979) mentioned success in "wattling" experiments, wherein bundles of willow slips were buried parallel to shorelines. Sprouting created a shield that protected bass nesting habitat from soil erosion and wind. However, attempts to improve the spawning success of largemouth bass in the windswept coves of Lake Carl Blackwell, Oklahoma, by forming breakwaters of tires, were unsuccessful (Clady and Summerfelt 1979).

59. During filling of Lake Oahe, fish stocks were dominated by species that preferred inundated littoral vegetation for spawning and nurseries--northern pike, yellow perch, carp, black crappie, white crappie, black bullhead, and certain minnow (June 1974). In the post-filling phase, most of these species decreased in abundance, and other species with less restricted reproductive requirements--goldeye, walleye, sauger, white bass, and freshwater drum--became plentiful. Reproductive success of bigmouth buffalo in Lake Oahe apparently depended on flooding of terrestrial vegetation (Moen 1974), as their numbers also decreased after filling. Prolonged inundation led to the disappearance of most terrestrial vegetation below the maximum water level. Land and water interactions continued erosion and restructuring, resulting in degraded spawning and nursery habitat (June 1974).

60. In Rathbun and Redrock Lakes, Iowa, a paucity of habitat greatly depressed the development of naturally sustained fish populations (Paragamian 1977). Predominant littoral habitats were windswept, and embayments contained little cover. Paragamian concluded that conditions

were unsuitable for spawning of species that lay adhesive eggs, because their spawning and nursery habitats were degraded.

61. Predator-prey relations. Year-class strength, as affected by mortality of larval and juvenile fishes, often is a function of available refuge and predator-prey interactions. The inundation of large areas of terrestrial vegetation has resulted in increases in the numbers of YOY largemouth bass (Kramer and Smith 1962; von Geldern 1971; Aggus and Elliott 1975), northern pike (Hassler 1970; Beckman and Elrod 1971), yellow perch (Chevalier 1977), black crappie (Ginnelly 1971), white crappie (Buck and Cross 1951), as well as carp, smallmouth buffalo, and bigmouth buffalo (Elrod and Hassler 1971). In addition to providing suitable spawning substrate, submerged vegetation presumably provided refuge and lessened the effects of predation.

62. In Bull Shoals Lake, flooded vegetation increased survival of largemouth bass during their first three months of life (Aggus and Elliott 1975). Predation apparently was the major cause of death. Aggus and Elliott (1975) found that the abundance of YOY largemouth bass in August was related to the number of acre-days of timber inundation earlier in the year. The presence of flooded vegetation had less effect on survival of YOY spotted bass and smallmouth bass than on that of largemouth bass in Bull Shoals Lake (Aggus 1979).

63. Strong year classes of any major predator may surpress the year-class strength of other predators. Jenkins (1975) concluded that it is virtually impossible to produce strong year classes of largemouth bass every year due to cannibalism (mostly by yearlings) and to the lack of submerged vegetation in some years. Swingle and Swingle (1967) noted that weak year classes of crappie occurred when a strong year class of largemouth bass had developed the previous year.

64. Reservoir managers have effectively used late summer and fall drawdowns (Keith 1975) to force prey fish from refuge in inundated vegetation or to physically concentrate them, thereby increasing their availability to predators. Fall drawdown of water in Ridge Lake, Illinois, resulted in improved predator feeding, larger bluegill, improved bluegill harvest, and increased growth of largemouth bass (Bennett et al.

1973). After drawdown, Heman (1965) observed increased growth of largemouth bass of all ages except YOY and found an inverse relation between the amount of flooded vegetation and feeding. Apparently decreases in protective cover after drawdown facilitate the transfer of energy (accumulated in small fish) to sport fish.

65. Structural complexity not only provides refuge for prey but also reduces foraging efficiency of predators (Murdock and Oaten 1975). Floating structures that reduce light penetration into the water beneath them may do the same (Helfman 1979). If prey engage in active predator avoidance, structured systems may facilitate such behavior, because predators are most effective in environments with little structure (Cooper and Crowder 1979). Prey may be more abundant, larger, and more diverse in heavily structured habitats. The question arises, "What is the optimum amount of structure for maximizing energy flow through sport fish?"

66. Jenkins (1970b) stated that too many trees may dilute the concentrating effect that facilitates angler harvest. Cooper and Crowder (1979) and Crowder and Cooper (1979) concluded that dense structure can reduce fish productivity by reducing the feeding effectiveness of predators and that in areas with little cover the prey biomass is small due to predation. A paucity of cover is common in cleared reservoirs where predators may easily overrun their prey base. On the basis of fish sampling in coves in August with rotenone, Jenkins and Morais (1978) found that about half of the 23 reservoirs sampled as part of a predator-stocking evaluation had prey deficits. Cooper and Crowder (1979) suggested, as did Eipper and Regier (1962), that intermediate structural densities provide the best environment for high sustained fish production. Swingle (1968) reported that fish production was increased 20 percent by the addition of brush to ponds. Similar increases in production have been observed after the addition of pine boards to pools (Pardue 1973) and the addition of tire structures to Smith Mountain Lake, Virginia (Maughan et al. 1976). Wege and Anderson (1979) observed faster growth of largemouth bass in ponds with structure than in those without it.

67. Pardue and Nielson (1979) found no significant increase in production of tilapia or bluegill after the addition of pine boards to

experimental ponds. They concluded that the addition of artificial substrate to increase production of fish seemed inappropriate in most management situations. However, Pardue and Nielson (1979) noted that in topographically simple environments, even small additions of substrate may substantially increase available structure and produce observable results. They discussed earlier findings of Pardue (1973) and cited activities such as retention of stumps or brush in new impoundments as likely ways to improve production.

68. Standing crop and harvest. Attraction and concentration of many sport fishes to structure, because of increased prey abundance, refuge, or spawning and nursery habitat, often improves harvest. Davis and Hughes (1971) showed that the presence of submerged trees decidely increased the local abundance of catchable-sized largemouth bass and black crappie. Other species (e.g., gar, buffalo, and bullhead) were more abundant in open water. Rotenone samples indicated that largemouth bass were concentrated in or near timber and large crappie in open water, at least in most seasons. In a large-scale study that compared standing crops of fishes in different habitats of Barkley Lake, Kentucky, Pierce and Hooper (In press) found standing crops of 2368 kg/ha in brush shelters, 968 kg/ha in tire attractors, and 690 kg/ha in control areas that lacked structure. The ratios of mean standing crop in brush structures to that in control areas were 10:1 for channel catfish, 61:1 for bluegill, 35:1 for largemouth bass, and 44:1 for white crappie. Fish-attracting structures in Barkley Lake were not particularly effective in concentrating a greater proportion of harvestable-sized fish, except for crappie (Table 1), but the structures did concentrate predators of all sizes.

69. The concentrating effects of structure also have been documented by comparing naturally timbered areas with cleared areas. The standing crops of fishes from two coves (one cleared, the other wooded) collected by the Kansas Fish and Game Commission in Tuttle Creek Lake, Kansas, illustrate that total standing crop and the total crop less gizzard shad were significantly less in the cleared than in the wooded cove (Table 2). Biomass was significantly less in the cleared than in the wooded cove for largemouth bass, crappie, buffalo, carp, river carpsucker,

Table 1

Effectiveness of Fish-Attracting Structures in Selected Areas of Crooked Creek Arm, Barkley Lake, Kentucky*

Type Fish	Harvestable Size, mm	Brush Attractors		Tire Attractors		Cleared Areas	
		kg/ha	% of Crop	kg/ha	% of Crop	kg/ha	% of Crop
Channel catfish	$\geq$ 254	166.9	74	67.2	77	16.8	75
Bluegill	$\geq$ 152	299.0	73	72.8	72	4.5	66
Largemouth bass	$\geq$ 254	38.1	97	22.4	100	1.1	100
White crappie	$\geq$ 203	430.1	87	123.2	77	4.5	40

* Data were modified from that presented in Table 2 of Pierce and Hooper (In press). Percent of total crop was calculated as weight of harvestable-sized fish divided by the total in selected areas.

Table 2

Concentrating Effects of a Wooded Cove versus a Cleared Cove in McIntire Arm, Tuttle Creek Lake, Kansas*

Species	Cleared Cove (C)		Wooded Cove (W)		
	Mean Standing Crop, kg/ha	Mean Wt, g	Mean Standing Crop, kg/ha	Mean Wt, g	Ratio W:C
Channel catfish	3.7	70.2	10.9	203.6	3.0
Flathead catfish	1.8†	64.3**	6.2	219.8	3.4
Sunfish	2.9**	8.3	10.7	9.5	3.7
Largemouth bass	0.9†	24.2†	4.9	54.1	5.4
Crappie	2.7†	30.1†	16.1	47.5	6.1
White bass	6.0	65.6	7.4	45.4	1.2
Walleye	0.7	170.0	0.8	485.8	1.1
Buffalo	15.2†	485.8	131.0	665.7	8.6
Gizzard shad	150.9	10.1††	322.8	5.9	2.1
Minnow	0.3†	0.9	0.7	1.1	2.1
Freshwater drum	14.5	19.1	16.2	25.2	--
Carp	10.2†	317.6‡	51.5	227.5	5.1
River carpsucker	6.7†	95.7†	38.5	190.0	5.7
Total crop	218.7†	--	617.3	--	2.8
Total crop less shad	65.0†	--	294.4	--	4.5

* Unpublished data of the Kansas Game and Fish Commission; notation of significance is based on Mann-Whitney test.
** Significantly less than in the wooded cove ($\alpha = 0.10$).
† Significantly less than in the wooded cove ($\alpha = 0.05$).
†† Significantly more than in the wooded cove ($\alpha = 0.10$).
‡ Significantly more than in the wooded cove ($\alpha = 0.05$).

and minnow (at $\alpha < 0.05$) and sunfish ($\alpha < 0.10$). Mean weights of largemouth bass, crappie, and river carpsucker ($\alpha < 0.05$), and flathead catfish ($\alpha < 0.10$) also were less in the cleared than in the wooded cove, though the mean weight of gizzard shad and carp was greater in the cleared than in the wooded cove. Perhaps smaller prey are more attracted to structure than larger prey, and their numbers in turn attract more and larger predators. Data available are too limited to evaluate this hypothesis.

70. Increased harvest is an obvious value of concentrating sport fish. Fishery workers have long agreed that standing timber left in the fluctuation zone of reservoirs attracts and concentrates sport fish to improve the catch of anglers (Parsons 1958; Jenkins 1970b). Calhoun (1966) observed greater catches of sport fish in timbered than in cleared areas of Lake Isabella, California. Timbered areas also received more fishing pressure. In Lake Kainji, Africa, about 10,000 acres were cleared at high cost, but early fishing experience suggested that yields per unit of effort were highest in shallows that had not been cleared (El-Zarka, In press, as cited by Dussart et al. 1972). Observations in Lake Kariba, Africa, were similar.

71. Burress (1961), who compared harvest statistics of anglers fishing in timbered and in open-water areas of Bull Shoals Lake, Arkansas, found a far greater harvest from timbered areas (3421 kg/ha) than from open water (126.6 kg/ha) in a 29-month study. The fact that anglers who fished in timbered areas took an enormous harvest, accompanied by an average catch of 1.25 fish per hour, indicated that fish were continually recruited from outside the timbered areas. Anglers caught fewer species of fish in timbered than in open-water areas, but the relative proportions of crappie, bluegill, and largemouth bass were the same. Eight species not represented in the creel of anglers who fished in timbered areas (bullhead, drum, sucker, rock bass, trout, warmouth, gar, and eel) were of little significance in the total harvest. Percent of successful anglers was similar for both areas (95 percent in timbered areas; 90.6 percent in open water).

72. Davis and Hughes (1971), who conducted a creel census of

anglers in timbered and open-water areas of Bussy Brake Lake, Louisiana, for three years, found that the presence of timber tended to congregate fishermen--50 percent of the total in the first year, 67 percent in the second, and 90 percent in the third, though trees apparently had no significant effect on the catch (kg/hour) of black bass, crappie, sunfish, or catfish. No estimates of harvest per unit area were made. Fishing success (the chance of catching at least one fish per trip) was consistently higher in timbered than in cleared areas--90 versus 79 percent in 1960-61, 87 versus 74 percent in 1961-62, and 86 versus 66 percent in 1962-63. The authors concluded that retention of some trees in reservoirs is desirable on the basis of increased fishing success.

73. Wege and Anderson (1979) found that catches of largemouth bass and bluegill were higher in ponds with structure than in those without. In Killdeer Lake, Ohio, the harvest of bass and sunfish was greater from areas near artificial reefs constructed of limestone or of limestone and tires than from nonstructured areas (Paxton and Stevenson 1979). Reefs made of limestone and piles of tires produced the highest catch per hour of bluegill, rock bass, and smallmouth bass. At similar reefs without tires, catches were dominated by green sunfish. Angler success in catching yellow perch was significantly higher in open water than near artificial reefs, with or without tires.

Artificial structures

74. A growing number of researchers are studying the effectiveness and practicality of man-made structures to improve fisheries. Results of certain studies were discussed in previous sections of this report. Most research seems to support the premise that some structures are more effective than others. Data are insufficient for biologists to determine which artificial structures provide the best return to fisherman in relation to cost and manpower needed to construct and maintain them. Valid comparisons of the effectiveness of inundated vegetation versus artificial shelters are lacking. Until such comparisons are made, widespread use of artificial shelters cannot be justified for all new impoundments. In new impoundments where structural habitat in the form of submerged timber, brush, or boulders can be retained without cost,

the value of adding elaborate artificial structures seems questionable. Most early artificial structures in the southeast consisted of no more than two or three trees cabled together and cabled to the reservoir bottom (Parsons 1958). If such simple structures are effective, their cost could be justified, but as Parsons noted, selective timber clearing may eliminate the need for installing brush-shelters in new impoundments. Attracting structures--first widely studied by biologists with the Tennessee Valley Authority (TVA) in the late 1930's and early 1940's (Prosser et al. 1979)--are widely used by TVA, and no doubt are successful in increasing fish harvest in older Tennessee Valley impoundments that were extensively cleared before they were filled.

75. Although artificial structures are valuable in bringing structure-oriented fish (e.g., black bass, crappie, and sunfish) and anglers together, problems with placement to avoid exposure of structures during drawdown, and periodic maintenance costs have inhibited their use (Jenkins 1974). As Calhoun (1966) stated, "California experience with brush shelters has been generally unsatisfactory. . . . An experimental program at Millerton Lake, a large fluctuating warm-water reservoir, proved expensive and unprofitable."

76. Several publications have reviewed and contributed to the existing information on the effectiveness of artificial structures in improving sport fisheries and are valuable references for further information. Construction from a variety of materials was described by Brouha and Prince (1973) and Wilbur (1974). Wilbur (1978) compared the effectiveness of attractors made from clay pipes with others composed of brush and cement blocks. Prince et al. (1975) emphasized research on species abundance, biological productivity, spawning, fish movement, and fishing success. The effectiveness and economics of artificial reefs were examined by Prince and Maughan (1978). Prince et al. (1979) discussed periphyton production, predator-prey relations, condition, and growth of reef fish. A collation of current research on fish responses to structure (principally artificial) was presented in a symposium conducted in 1978 by the North Central Division of the American Fisheries Society (Johnson and Stein 1979).

77. As reservoirs age, terrestrial vegetation in littoral areas eventually deteriorates, and the use of artificial shelters can then become an economically viable management technique. The structural integrity of original timber or brush varies mostly with size and seasonal inundation; large trees last from 30 to 40 years, and permanently submerged trees last much longer than those dried each year. In new reservoirs that lack timber (e.g., in prairie regions), the preimpoundment construction and annual refurbishment of artificial shelters may be justified.

Inundation tolerance

78. Knowledge of the tolerance of terrestrial vegetation to inundation is essential to management of "green-tree reservoirs"--i.e., reservoirs wherein water levels are managed to maximize retention of living trees in the fluctuation zone. When flooded in the spring, living vegetation not only seems to improve reproductive success of nest-building fishes, but also provides spawning and nursery habitat for many more years than does dead vegetation. The volume of literature on inundation tolerance is large. Moyle (1958), who reviewed early literature dealing with effects of water level on plant growth, determined the survival of many trees and herbaceous plants in flooded areas. Much of his information was taken from an excellent study by Hall et al. (1946). Yeager (1949), who also conducted an extensive study of flooding effects on different species of trees, noted that virtually all trees had died after being permanently flooded to a depth of 20 in. for 6 years. Harris (1975), who studied flooding effects on Keystone and Oologah Lakes in Oklahoma, made the following observations after trees had been inundated for 73 and 67 days of the growing season in the respective reservoirs: (a) flood damage was most severe within the first 10 ft above normal pool; (b) most trees died when completely submerged; and (c) though 80 percent of the trees less than 10 in. in diameter (at breast height) or less than 25 ft tall died when significantly stressed, larger trees showed no visible stress other than reduced growth. He suggested that trees and shrubs planted in flood zones of recreation areas should be limited to water-tolerant species such as green ash, sycamore, cottonwood,

buttonbush, willow, mulberry (fruitless), silver maple, bald cypress, and river birch. Most of the literature on inundation tolerance indicates that flooding during the dormant season has little effect on survival, but that flooding during the growing season significantly increases mortality. Bell and Johnson (1974), who determined tolerances to growing-season inundation for 24 tree species in Illinois, suggested setting a limit of 30 days' inundation during spring and summer to ensure survival of all trees around reservoir margins.

79. Teskey and Hinckley (1978a, b, c, d, e) provided the most recent and extensive review of literature on inundation tolerance. Their five papers concern woody plants in five regions of North America, by dominant forest type. Information collated is useful as a quick reference to species tolerance. For example, Teskey and Hinckley (1978c) gave an extensive list of woody plants and their percent survival under constant flooding. Variables considered were tree species and size; submersion type (total, partial, or soil saturation); time of year (dormant or growing seasons); and duration of flooding. Perhaps the most valuable aspect of their data collation is that all entries are referenced. For each region, the authors present a "species tolerance list" that characterizes trees as very tolerant (can withstand flooding for two or more growing seasons), tolerant (can withstand flooding most of one growing season), intermediately tolerant (can withstand flooding for 1-3 months of the growing season), and intolerant (cannot withstand flooding for less than one month during the growing season).

PART III: GUIDANCE AND RECOMMENDATIONS

Reservoir Filling

80. Strategies for filling reservoirs are few and their applicability depends heavily on factors related to basin morphometry (primarily size and depth), precipitation, inflow, discharge, and use requirements. In some reservoirs, rates and time of filling can be controlled by manipulating discharge. However, impoundments with a high ratio of discharge to volume often fill quickly during months of heavy precipitation. Persons concerned with the water quality after filling often have recommended that reservoirs be filled and flushed several times to remove wood flotage, soluble nutrients, and fine particulate matter (e.g., Sylvester and Seabloom 1965). In reservoirs with water exchange rates exceeding 1 year, such a flushing procedure would not be practical. "Stage filling"--the filling of reservoirs in well-defined stages--is practical only in a few situations where the proposed reservoir will be large and where use requirements by nearby populations (water supply, recreation, irrigation, or power generation) will not exceed what can be provided during early stages.

Minimum pools

81. Minimum pools often are established at the lower limit of efficient power generation ("rated pool" of hydropower reservoirs), to provide an amount of water necessary for survival of fish populations (Nelson et al. 1978), or to provide for consumptive uses (water supply and irrigation in storage or hydropower-storage impoundments). Nelson et al. (1978) reported that minimum pools ranged from one to twelve percent of total capacity in nine reservoirs. All projects reviewed with established minimum pools were considered successful or marginally successful in protecting fisheries.

82. Butler (1962) realized that satisfying fishery needs required compromises with other project purposes. Using area-capacity curves, he described a method of defining a minimum pool at which the ratio of area to volume was maximized. Theoretically, increased surface area increases

productivity and oxygen exchange at the air-water interface. According to Butler (1962), one should plot area versus elevation and volume versus elevation on the same figure, with appropriate adjustments of volume and area scales on the ordinate. Maximum surface area with the least volume may be located on the capacity curve as the midpoint of the minimum-radius arc (minimum radius of curvature). Capacity at this point is usually a small percentage of maximum storage; at lower elevations, minimum pools are set at the expense of surface area; at higher elevations, minimum pools are set at a proportionally greater expense to water storage.

83. As Butler suggested, his method is only a tool and other factors should be considered. Three such considerations are future reservoir operations, basin shape, and water quality. If reservoirs are to be drawn down in the winter (which is typical of many hydropower and flood control reservoirs), the elevation of the minimum pool may not be critical because cold water holds more oxygen and reduces respiration (and therefore oxygen consumption). By contrast, if surface area at minimum pool is small in relation to depth, summer or early-fall drawdown may impose oxygen stress, especially for basins sheltered from the wind. In shallow windswept impoundments, the establishment of a minimum pool probably is not critical, as surface area at low water levels is typically large in relation to volume. Highly productive, nutrient-rich reservoirs should be assigned minimum pools with greater surface area than those assigned to oligotrophic reservoirs, especially if summer drawdowns are anticipated. Plans should be made to gradually increase the size of minimum pools as reservoirs age and eutrophication advances. Success or failure of minimum pools to protect fishes in nearby reservoirs of the same drainage may give insight into the pool size required.

Stage filling

84. Stage or incremental filling of reservoirs is a new technique, and to date more reservoirs probably have been "stage filled" by accident than by design. For example, Beaver Lake, Arkansas, was filled essentially in three stages, corresponding to the relatively dry years of 1964, 1965, and 1966. Results of stage filling have not been evaluated

quantitatively, though Nelson et al. (1978) stated that Melvern Reservoir, Kansas, which was stage-filled over three years, initially produced good year classes of northern pike. To attribute good year classes of northern pike to stage filling may be presumptions, inasmuch as strong year classes usually occur in the early years of most impoundments, regardless of how the reservoir was filled. Nevertheless, stage filling could potentially increase fish production in two ways--trophic enhancement and enhancement of spawning and survival.

85. Trophic enhancement is affected by rising waters that inundate terrestrial areas containing large quantities of nutrients and detritus. Stage filling allows the trophic system more time to assimilate available energy, especially during early stages when small, productive pools are present. These small pools are characterized by high rates of water exchange, high ratios of epilimnion versus hypolimnion volume during stratification, shallow mean depth, and high quotients of drainage area to volume. Under normal filling, small productive pools are eliminated as rising waters quickly transform these shallow areas into unproductive deep waters.

86. Spawning and survival enhancement is affected by the successively renewed inundation of terrestrial vegetation which provides new, highly productive spawning and refuge sites that replace spawning and refuge areas that may have deteriorated during the preceding stage due to erosion or decay of herbaceous plants. Stage filling may increase the strength of several early year classes because more fishing pressure per unit of area increases harvest of recruits (potential predators). Periodic and significant increases in water level also should greatly increase YOY survival by providing refuge and food for fish of all ages.

87. Though stage filling could be a very effective tool, it is seldom practical. For example, the development and success of recreation facilities such as parks, boat ramps, and marinas depend strongly on water level. Provision of such facilities at all stages could be expensive in some reservoirs, depending on basin relief and existing access at different elevations. Factors that affect the demand for facilities (e.g., projected annual visitation or the proximity of the reservoir to

urban areas) should provide insight into the need for permanent recreation facilities during early stages of inundation. Reservoir size, type, and rate of water exchange also determine the practicality of stage filling. The reservoirs best suited for stage filling are large (>4,000 ha) storage impoundments. (In terms of prolonging initially high production of fishes, the larger the reservoir is, the better.) Very large impoundments (>20,000 ha), where immediate needs for water are low, can be filled in a number of stages, and each new pool held for several years, before filling is continued. Nelson et al. (1978) cited Millican Lake, Texas, as an example of a large reservoir for which such a plan was developed. This plan called for incremental filling every 10 years for 40 years. Although such a plan clearly would not be practical for hydropower reservoirs (where increasing capacity improves efficiency of generation) or for some flood-control impoundments (where yearly filling is expected to reduce downstream flooding), it could increase the duration of the productive period by a factor of five in storage impoundments.

88. A major advantage of stage filling is that it greatly increases flexibility for coping with unforeseen events (Nelson et al. 1978). Filling schedules can be reviewed periodically to ensure that available pools provide sufficient water to meet increased demands for water supply, irrigation, navigation, or recreation. Early and flexible plans are essential to successful stage filling. Implementation of stage filling may be hampered by variability of runoff from the watershed or by problems in obtaining land (Nelson et al. 1978).

89. A logical way to establish pool elevations at successive stages for reservoirs with mean depths of 6-18 m is to divide area at maximum pool by the number of stages proposed. Because of the relation of area to volume, this technique will result in more small productive pools where the ratio of area to volume is relatively large. Successive increases in water level will result in an exponential increase in mean depth. The number of stages will vary with plans for other uses, but there should be at least three stages.

90. In steep-sided, deep basins--mean depth $\geq$ 18 m--more stages are warranted because these reservoirs are more likely to establish a

thermocline (thereby locking up nutrients and detritus in the hypolimnion during productive, warm-weather months) and have less littoral area (productive shallowwater areas above a depth of ca. 6 m, for fish feeding and spawning) than shallow, gently sloping reservoirs have. Deep reservoirs should be filled to pools defined by depth (the factor most limiting their fishery productivity), rather than by area. Ideally, intervals between consecutive stages should not exceed the depth of the anticipated thermocline--or from 6 to 9 m, when other data are not available.

91. In large, shallow basins (mean depth > 6 m), fewer increments of filling appear to be required, as even relatively large increases in area or depth will not limit the availability of inundated nutrients, detritus, fish food, or spawning sites. On the other hand, in some prairie reservoirs (e.g., Lake Oahe, North and South Dakota, and many Soviet impoundments) the ultimate limiting factor to production by initial populations of fish was available spawning habitat. Initially, grass and other herbaceous plants served as excellent sites, but after a few years these sites deteriorated or were silted over. Therefore, more increments of filling would ensure more new spawning and nursery grounds. Stages in shallow prairie reservoirs probably are best set on the basis of establishing as large an area as possible over a water depth of 2-3 m.

92. If vegetation has been mapped, examination of areas between two contour lines that are 5 to 10 m apart may aid in the selection of successive stages. Selection of stages at areas with the greatest density of vegetation between two elevations should help to maximize fish production by providing more spawning and nursery habitats and increasing production by animals at lower trophic levels. When a heavily vegetated belt is recognized, attempts should be made to fill to the upper elevation, therby covering desirable habitat with water to a depth of 5-10 m.

93. Time between consecutive stages usually is based on needs other than fishing, but intervals of less than one year will do little to improve fish production. On the basis of available literature, productive fisheries generally last from 5 to 10 years. Therefore, stage filling will be most effective in prolonging productive fisheries when the time between stages approaches the life expectancy of the productive period.

For example, a reservoir filled in two eight-year stages could feasibly produce 16 years of good fishing. One year between stages should improve the fishery, but would not be as effective as two years because of the adverse predator-prey relations that might develop between two strong consecutive year classes of predators. Biologists who have studied water levels seldom have observed two strong year classes in succession even after the most desirable manipulation of water level. Keith (1975) suggested that occasional drastic drawdowns at intervals of 3, 5, or 10 years were more effective in increasing fish production upon refilling than lesser annual drawdowns.

Timing and fluctuation control

94. Seasonal timing of inundation (staged or complete) has a significant impact on the species composition and productivity of reservoir fish. During filling, the magnitude and seasonal aspects of water-level fluctuations also may affect reproductive success and production by flooding or dewatering large quantities of terrestrial fish foods. Winter filling may result in poor use of newly inundated nutrients and foods by organisms of all trophic levels due to the depressing effects of low water temperatures on bioenergetic processes (e.g., consumption and digestion). In reservoirs that are rapidly dewatered during spring and summer spawning--"flushing" as recommended by Sylvester and Seabloom (1965)--fisheries will not develop to their potential.

95. Inasmuch as most riverine fishes have evolved reproductive strategies cued to normal seasonal cycles of flooding, man can enhance fisheries by providing these conditions during filling. Benson (1973) recommended the following manipulations to benefit fish reproduction in Missouri River impoundments. Water levels should be allowed to rise to desired levels by early spring; held nearly constant, with only minor increases, from 1 April through 1 July; and lowered after 1 July to concentrate forage, thereby increasing survival of young predators. Other biologists who have studied effects of water level have made similar recommendations (see Fraser (1972)). Some recommendations have called for filling during the autumn or winter (e.g., West Point Reservoir, Alabama and Georgia) to avoid establishment of an undesirable overabundant

population of rough fish (primarily carp). However, inasmuch as spawning of carp and other rough fish overlaps that of most valuable species, the development of filling procedures to benefit spawning of valuable species, while hindering the spawning of undesirable species, does not seem feasible. Published data to evaluate the effectiveness of such filling strategies are lacking.

96. Knowledge of spawning and nursery requirements of fishes in the proposed reservoir is essential for the development of effective strategies of water-level manipulation (Benson 1976). Similar knowledge is required to develop effective filling strategies for new reservoirs. Carlander (1969, 1977) listed temperature requirements for spawning of many sport and commercial fishes. Time of spawning varies directly with temperature, and therefore temperature is more reliable than time of year as an index to spawning, given variations in water temperature with latitude. In reservoirs with warmwater fisheries (black bass, sunfish, catfish, crappie), virtually all important forage, sport, and commercial fish spawn when temperatures are between 11 and 22°C. In reservoirs dominated by coolwater species (northern pike, walleye, sauger, yellow perch), the temperature range is from about 5 to 17°C.

97. After predicting which species will dominate the fish community in the proposed impoundment (based on information from similar impoundments at the same latitude), water temperatures required for spawning should be compared with seasonal temperatures in the river (available in "Water Resources Data--Annual Reports," U. S. Geological Survey) to estimate when the earliest spawning will begin. If possible, spawning dates also should be approximated by examining fishery data collected from nearby reservoirs that have temperature regimes similar to that anticipated in the new reservoir. On the basis of monthly river discharge, the time when filling would have to be started to attain the desired pool elevation by spawning time should be estimated. When water temperatures rise to the critical limits (11°C for warmwater species; 5°C for coolwater species), water levels should be held constant or allowed to rise slowly. Excessive runoff can be handled to some extent by establishing larger pools (stage filling) or increasing discharge to maintain desired levels.

Unexpected low runoff is another problem altogether, and the only recourse is to let water levels rise slowly throughout the spawning period as water becomes available.

98. A fall drawdown to increase forage for young predators, as recommended by Benson (1973) and others, should not be necessary in a new impoundment, inasmuch as production usually greatly exceeds that in older reservoirs. On the other hand, such a drawdown may effectively control populations of rough fish. Decisions to employ fall drawdown should be based on estimates of total standing crop and an index to the ratio of available prey to predators--e.g., the predator-prey model of Jenkins and Morais (1978) or to the Young of the Year/Standing Crop (Y/C) ratio of Swingle (1950).

Clearing of Reservoir Basins

99. Sylvester and Seabloom (1965) reported that literature dealing with the effects of site preparation was sparse. Site preparation has ranged from removal of all timber, secondary vegetation, and debris to partial clearing between specific elevations with timber retained in selected coves, embayments, or shallowwater areas. Many reservoirs constructed before 1955 were cleared extensively to avoid mosquito or water quality problems. In time, more plans for selective clearing were developed, as malaria epidemics became infrequent or were eradicated, as costs of clearing became prohibitive, and as public concerns for providing habitat for fish and wildlife increased.

100. The principal objective for mosquito control is to clear the basin so that the surface and shoreline are clean (Federal Security Agency et al. 1947). Completely submerged timber usually is not removed but anchored to the bottom to control flotage. Mosquito abundance is directly related to the number of structures intersecting the air-water interface, and control has been most successful in reservoirs where standing timber, flotage, and other surface-breaking structures were held to a minimum. Additional site preparation often involves construction of drainage ditches to ensure that all marginal pools, sloughs, and

depressions fluctuate freely with the main lake.

101. Several researchers who have examined effects of soils and vegetation on water quality have advocated complete clearing, removal of herbaceous plants, and even stripping of soils to prevent degradation of water quality (e.g., Hammerton 1959; Allen 1960; Sylvester and Seabloom 1965; Smith and Justice 1975; Campbell et al. 1975; Ball et al. 1975). On the basis of leaching rates from different plant species and their densities within reservoir basins, Ball et al. (1975) developed a methodology for predicting the impact of original vegetation on postimpoundment water quality. Smith and Justice (1975), who studied effects of clearing on arctic and subarctic reservoirs, provided a technique to evaluate the economics of various degrees of clearing. Their method was based primarily on the annual costs of water treatment as a function of clearing depth over the first 10 years of impoundment. Campbell et al. (1975) found that the effects of soil stripping were most evident in the early history of impoundments. In reservoirs with 5 percent organic soil and under aerobic conditions at 25°C, the beneficial effects of soil stripping were relatively short-lived. After about 35 days, water quality over stripped and unstripped samples was virtually indistinguishable. Under anaerobic conditions, as in the hypolimnion of a thermally stratified reservoir, beneficial effects of soil stripping lasted much longer that those observed in aerobic situations.

102. Parsons (1958) recognized that most controversy about timber clearing arose over the location and extent of timber to be left along shorelines. By 1958, most biologists agreed that timber left standing in deeper portions of reservoirs was not harmful and that timber in the fluctuation zone would attract sport fish.

103. According to Hulsey (1959), retention of large uncleared areas in the fluctuation zone decreases costs of clearing, reduces wave action and erosion of shoreline, produces CO_2 (after decomposition) which helps flocculate colloidal clay turbidity, increases surface areas for attachment of periphyton and other organisms and thereby increases productivity, and provides habitat diversity for fish. Hulsey recognized the necessity of clearing for access and recreation, but strongly

questioned much of the earlier clearing that had been proposed in behalf of public health. To improve fisheries, Hulsey recommended clearing of harvesting basins, netting areas, boat lanes, and public access and adjacent areas.

104. Jenkins (1970c) described the problem of optimum clearing as "knotty," stating that the most productive patterns for clearing were those in which timber was retained in selected arms of deep reservoirs with boat paths provided for access or those in which dispersed blocks of timber were retained in shallow reservoirs. He emphasized that timber left completely submerged in deep water (>10 m) contributes little to fish production or angling success and interferes with the operation of devices for population sampling and rough-fish control that are frequently used in fishery research or management. Also, he concluded that the principal value of a veritable forest of exposed tree tops lay in the protection it afforded to fishermen from disturbance by high-speed boats.

105. Weber (1968), who developed a plan for clearing Narrows Reservoir, Colorado, considered a number of factors, including aesthetics, navigation, topography, and recreational uses. He recommended retention of timber near but not within sight of recreation areas, thus providing ready access to anglers without aesthetic degradation. Because of the topography of Narrows Reservoir, no coves or embayments were expected to develop. Therefore, he suggested retention of timber in sheltered belts along the river bottom and in 0.4- to 0.81-ha blocks. Blocks of trees were recommended to afford fishermen protection from other boaters and to provide more edge (areas that are easier to navigate and fish). Only trees greater than or equal to 45.7 cm in diameter and 9.1 m high were retained, as these trees would last longer than smaller trees and would be visible over a wider range of lake levels.

106. According to Calhoun (1966), California biologists generally prefer the retention of cover in warmwater reservoirs. Procedures such as the one developed for selectively clearing Oroville Reservoir (Fischer et al. 1964) can save substantial sums of money. On the other hand, cover retention in coldwater reservoirs does not appear to benefit salmonid

fisheries, and therefore clearing has been encouraged to facilitate angling and other recreation.

107. Nelson et al. (1978) observed that selective clearing may refer to clearing of selected areas (as in the present discussion) or to retention of selected tree species. Water-tolerant trees, as listed by Teskey and Hinckley (1978a, b, c, d, e), often are retained in public access areas or parks where less tolerant species would die and become unsightly. Because they can tolerate several months of inundation during the growing season, these trees can greatly enhance the aesthetic qualities of shorelines in recreational areas and protect shorelines from erosion.

108. In 19 reservoirs where selective clearing was employed, Nelson et al. (1978) classified 11 as successful and 6 as marginally successful. Because selective clearing has little direct cost associated with it (compared with the cost of complete clearing), evaluation of success was rather subjective, based primarily on confidence factors (high, medium, or low) that were used to rate soundness of habitat and population predictions.

109. Ball et al. (1975), who reviewed the clearing rationale of the Bureau of Reclamation and U. S. Army Corps of Engineers, concluded that clearing policies were designed primarily to prevent clogging of control works and outlets and to provide for safe, efficient reservoir operation. Enough clearing is done to provide adequately for public safety and health, particularly in water supply reservoirs. Secondary considerations include fish and wildlife needs, boating, fishing, and other forms of recreation. In general, the only materials removed from basins are those that will increase construction costs, create hazards, or cause serious pollution problems. Reservoirs are completely cleared if complete clearing is considered cheaper than providing water treatment to offset the polluting effects of inundated soils, vegetation, and organic debris during the first 10 years of impoundment.

110. Clearing strategies differ for three reservoir zones (Ball et al. 1975). The bottom zone (Zone 1), which is located below an elevation 1.52 m beneath minimum pool, seldom is cleared, except for areas

adjacent to the operating works at the dam. The middle zone (Zone 2), which extends from 1.52 m below minimum pool to the top of the spillway gates, usually is cleared of all trees and brush more than 1.52 m high or 5.10 cm in diameter (near ground level). Trees and stumps are uprooted or cut off at ground level, and all combustible materials more than 10.16 cm in diameter are burned and buried with at least 0.61 m of cover. The narrow upper zone (Zone 3), which extends above the elevation of the spillway gates, is not cleared except in areas required for permanent access.

111. The following terms are used in the remaining sections to describe areas of clearing in reservoir basins:

- a. Minimum pool--the minimum volume of water required for efficient power generation, protection of fishery resources, and other uses.
- b. Multipurpose pool--a volume of water above minimum pool used for power generation, water supply, recreation, or other uses. (Examples include summer, normal, and conservation pools.)
- c. Flood pool--a volume of water above the top of multipurpose pool and within a zone reserved for flood control.
- d. Maximum pool--a volume of water at the top of (and retained by) the spillway gates (top of flood pool).
- e. Fluctuation zone--the area of a reservoir basin between minimum- and flood-pool elevations.
- f. Surcharge zone--a narrow zone that extends above the maximum pool elevation, which may be inundated briefly when floodwaters rise above the spillway gates.

Clearing below minimum pool

112. General considerations. Vegetation below minimum pool probably does not affect fish production and harvest except in reservoirs where nutrients, detritus, and structure are accessible to reservoir biota (e.g., during turnover in deep reservoirs, in shallow reservoirs, or in new impoundments during early stages of filling). In deep reservoirs, removal of herbaceous and woody vegetation below minimum pool probably would not limit fish production but could improve water quality in the hypolimnion during stratification.

113. In most reservoirs, clearing below minimum pool should be

limited to that required to provide for efficient operation and safe navigation. Timber should be removed from areas adjacent to outlet structures to reduce chances of clogging. Trees projecting above an elevation 1.52 m below minimum pool should be topped at that elevation so that they will not interfere with boating when water levels are low. Exceptions should include timbered coves, small embayments, or selected 0.5- to 1-ha blocks within about 10 m of the shoreline at minimum pool. Retention of standing timber in these areas would enhance the fishery (by concentrating certain fishes for harvest and providing anglers refuge from speedboaters or water-skiers during low water) and still provide plenty of area for boating. Narrow boating lanes (4-6 m wide) should be cleared in coves, embayments, or large blocks of timber to provide access for anglers (Burress 1961; Dussart et al. 1972).

114. Additional clearing below minimum pool is recommended only in reservoirs that could develop serious water-quality problems (e.g., algal blooms, low dissolved oxygen concentrations, and noxious odor or taste caused by highly fertile soils and luxuriant vegetation) or in impoundments where conditions are suitable for the inclusion of a harvesting basin (described below).

115. Water quality. The potential for serious water-quality problems can be predicted by preimpoundment testing of soils and vegetation (Ball et al. 1975) or by ecosystem modeling of nutrients and algae. Economics of clearing may be determined by comparing estimates of clearing cost versus cost of water treatment over the first 10 years of impoundment (Smith and Justice 1975).

116. Harvesting basin. In certain reservoirs, a harvesting basin (Hulsey 1959) can be a valuable asset to the management of fish populations. A useful management technique for some small reservoirs involves a periodic (3-10 years) drawdown to a residual harvesting pool, thereby concentrating fish stocks and facilitating their manipulation or harvest. By harvesting or eliminating most of the large rough fishes, managers can alter the trophic structure of impoundments to improve production of sport fishes. Only the young of large rough fish (e.g., gizzard shad, carp, buffalo, and redhorse) are available as sport fish prey, and many

outgrow potential predators and act as an energy sink (i.e., their maintenance and growth requires more energy every year, but their biomass is unavailable as food for sport fish and seldom is harvest by man). A cleared harvesting basin permits efficient harvest or removal that in turn helps to "redistribute" the biomass of large rough fish (after spawning of those remaining) among smaller sizes that are more available to predators. A harvesting basin also permits the use of deepwater samplers and other research equipment during times of low water.

117. Practicality of a harvesting basin depends on reservoir size and prospective use. Harvesting basins probably would not be practical for reservoirs larger than 1500 ha or for most hydropower reservoirs. Drastic drawdowns of large reservoirs to a harvesting pool would severely restrict all other uses (e.g., power generation, recreation, water supply), and additional costs for clearing could be high. In reservoirs much larger than 1500 ha, manipulation of the large stocks of fish probably would be too expensive. Desirability and potential use of a harvesting basin should be ascertained early in the planning process.

118. A harvesting pool should not exceed 20 percent of the surface area at the top of multipurpose pool and could be much less, depending on basin shape (Hulsey 1959). In shallow reservoirs, harvesting basins may compose 5 percent of the surface area at the top of multipurpose pool, and in most reservoirs they compose less than 30 percent of the surface area at minimum pool.

119. When a harvesting basin is warranted based on reservoir size and potential use, an elevation at which surface area is from 5 to 20 percent of that at the top of the multipurpose pool should be selected. Although small basins probably are more effective than large ones for management purposes and cost less to clear, care should be taken to ensure that the harvesting basin is not so small that it fills with sediment in a few years. The life expectancy of a harvesting basin can be estimated by dividing basin volume by expected annual rates of sedimentation. Harvesting basins should be cleared completely so that the bottom is smooth. Usable timber should be harvested and larger wood debris burned or removed. A deep outlet that will permit draining to the

harvesting-pool elevation must be incorporated into the dam during early phases of construction.

Clearing between minimum and maximum pools

120. General considerations. Selective retention of brush and timber between minimum- and maximum-pool elevations is needed to provide habitat for structure-oriented fishes during most of every year. Traditionally, most reservoirs have been completely cleared in this zone; timber and brush are then available to fish only during brief periods of flooding, when floodwaters rise above maximum pool and inundate vegetation in the uncleared surcharge zone.

121. Many practical strategies for clearing between minimum and maximum pools have been developed, but to date there have been no studies to compare the effectiveness of different amounts or patterns of timber retention. Selectively cleared reservoirs usually have had timber retained (a) in blocks along shorelines or in open water, (b) in shoreline clusters of 3 to 10 trees, (c) along the border of old stream channels, or (d) in coves and embayments. All of these timbered areas benefit fisheries when used in appropriate situations. Depending on basin morphometry within the fluctuation zone, combinations of the above patterns of timber retention may be used, thereby providing fishermen with a greater variety of timbered fishing sites.

122. Clearing of the fluctuation zone in hydropower and flood-control reservoirs should be designed to complement management techniques for enhancing fisheries by water-level manipulation. For example, timber could be retained in selected sites in the upper 80 percent of the fluctuation zone and completely cleared from the lower 20 percent, where percentages are based on depth; e.g., $0.80 \times (E_T - E_{min})$, where E_T is the top of the multipurpose pool and E_{min} is the minimum-pool elevation. Then lake drawdown would decrease reservoir size and available cover, thereby concentrating prey fishes and exposing them to predators. Sport fish would benefit by increased food availability, especially if drawdown occurred in the fall when available prey often is scarce. Selective timber above the dividing elevation will provide structural

habitat in productive shoreline areas during most of the summer.

123. The upper portion of the fluctuation zone should be selectively cleared as follows:

- _a_. Gradually sloping areas and embayments from the top of multipurpose pool to 10 m below. These areas are typical of shallow impoundments and the upper reaches of deep reservoirs. Trees should be retained in clusters of 5 to 15 or in 0.1- to 1-ha rectangular blocks and in larger blocks in windswept or waveswept areas to increase shelter for fishermen. Clusters and small blocks of trees may concentrate more fish than large blocks but should be retained only on the leeward shore in wide sections of the reservoir. Narrow boating lanes (4-6 m wide) should be provided in larger blocks of timber to provide access to fishermen. At the multipurpose pool, the surface area of all clusters and blocks of timber should not exceed 40 percent of the surface area overlying a depth of 6 m. Where possible, bands of trees should be left along old creek or stream channels to mark these productive fishing sites for anglers.

- _b_. Coves. Deep dendritic reservoirs usually have many coves in the fluctuation zone. Most are too narrow for safe speedboating but ideal for fishing. Trees should be left in ravines and canyons from maximum pool to 10 m below the multipurpose pool, except for boating lanes (4-6 m wide) cleared in the middle of all adjoining ravines. This procedure would provide timber and access lanes at many lake elevations and help zone the lake for different forms of recreation. Trees in coves adjacent to recreation areas should be cleared only when they will seriously degrade aesthetic qualities of the area. It is important to have good fishing sites in proximity to parks and recreation areas for the convenience of all anglers.

- _c_. Deep areas. To provide structure at many lake elevations, rectangular blocks of timber with the long axis perpendicular to the shoreline should be retained. These blocks of timber should be 50-100 m wide and extend from maximum pool down to an elevation corresponding to $0.20 \times (E_T - E_{min}) + E_{min}$. Timber visible along the shore will serve as a marker to facilitate the location of submerged timber by anglers. The distance that standing timber (i.e., timber protruding above the water) extends from the shore at any elevation will vary with the slope of the bottom and tree height. In narrow portions of the reservoir, the distance that standing timber extends from the shore may severely limit safe navigation. Unless practical sites are selected, standing timber

extending too far from shore may have to be topped to provide sufficient open water. Practical sites usually are those which indicate the following relation at multipurpose pool:

$$W \geq \frac{(h + 5)}{0.2|b|} \tag{1}$$

where

W = reservoir width perpendicular to the proposed site, m

h = maximum tree height, m

b = average bottom slope

Width and mean slope of the bottom at the proposed site can be readily obtained from topographic maps, and estimates of tree height need not be exact (± 5 m of the actual value). No more than one block of timber should be retained per kilometre of shoreline, and, when possible, a majority of the blocks should be situated on the leeward side of the lake to help reduce wind-induced turbulence, especially in areas with strong prevailing winds.

124. The clearing of reservoirs that fluctuate little (e.g., many storage and mainstream hydropower or flood-control reservoirs) differs from the clearing of fluctuating reservoirs only in the depth of clearing. Timber should be retained only to a depth 6 m below the anticipated average elevation of summer pool.

125. Special considerations. In prairie reservoirs or other impoundments in areas largely devoid of trees, emphasis should be placed on water-level management, retention of all herbaceous vegetation, and the formation of artificial structures in the fluctuation zone. Effective structures can be made by cutting dispersed trees, making piles of 3 to 10 trees, and anchoring the piles to the bottom in areas 6 m below the top of multipurpose pool. Otherwise, lone trees will do little to concentrate fish and will be wasted. Methods for building and evaluating the economics of artificial structures made of brush, tires, pipes, and other materials have been presented by several biologists (see citations under the heading "Artificial structures," Part II).

126. Recreation areas, parks, and sites of permanent access in the

fluctuation zone should be completely cleared of all but large water-tolerant trees (Teskey and Hinckley 1978a, b, c, d, e) that will be inundated to a depth of 2 m or less for no more than 2 months during the early spring and summer. Harris (1975) recommended a number of trees ideal for planting in recreation areas in the upper fluctuation zone of reservoirs. If appropriate species are retained, none need be planted, and ultimate costs can be reduced.

127. Herbaceous vegetation which usually is retained in new reservoirs should not be removed because it is essential to the rapid development and maintenance of high fish production during early years of impoundment. Detritus from these plants provides food directly to many animals (detritivores) and thereby shortens the food chain to sport fish and increases the efficient of energy flow. Nutrients released to microfauna and algae also increase the food available to animals of all higher trophic levels, including fish.

Clearing above maximum pool

128. According to most strategies, clearing of the surcharge zone above maximum-pool elevation is limited to recreation areas, parks, or areas of permanent access. Trees in this zone rarely are inundated for more than a few weeks during the growing season, and as a result, few of them die and become unsightly. Retention of vegetation in the surcharge zone benefits fish production by reducing erosion throughout the year, and when flooded in the spring, drowned animals and accumulations of leaf litter provide food for invertebrates, YOY, and adult fish. Because these trees seldom die from inundation, they often provide these benefits throughout the life of the impoundment.

Evaluating Alternatives

129. Although no methods have been developed to evaluate clearing or filling strategies with respect to their effectiveness in improving reservoir fisheries, a multiple-regression model holds promise for the future. Indices of clearing (e.g., percent of the basin area without timber) and filling (e.g., annual increase in surface area or mean depth)

may explain some of the variation in the standing crop and harvest of certain fish. Coupled with some of the other variables that affect biomass and harvest of fish (such as use, area, mean depth, maximum depth, outlet depth, thermocline depth, water-level fluctuation, storage ratio, shore development, TDS, chemical type, and growing season--Jenkins 1968, 1970a), the resulting multiple-regression model may improve the overall prediction of standing crop and harvest and help to delimit alternate strategies for site preparation and filling. Variation in crop and harvest due to other abiotic variables could be standardized and then the effects of clearing and filling clarified.

130. A preliminary survey of fishery data at the office of the National Reservoir Research Program revealed that standing crop data during early impoundment are available for 54 reservoirs, 36 of which are Corps of Engineers impoundments. Harvest data are available for 48 reservoirs, 28 of which are Corps impoundments. Descriptive data as used in the multiple-regression studies of Jenkins (1968, 1970a) also are available for most of these reservoirs.

131. Correspondence with various Districts revealed that the collation of appropriate clearing and filling data would require considerable effort. Memoranda concerning design and clearing, as well as other information from Districts, indicate that data on clearing and filling are available for most of the Corps reservoirs, but that these data frequently are scattered among several memoranda (some of which are not available) and are rarely in a usable form. Filling and clearing data for most municipal, state, and private impoundments usually are difficult and sometimes impossible to obtain.

132. Any evaluation of clearing or leaving timber in place should include consideration of navigation and recreational usage as well as fish production and water quality.

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